GERMINATION AND DORMANCY OF *ARTHROPODIUM CIRRATUM* SEEDS

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ABSTRACT

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Seed dormancy characteristics and environmental limitations on seed germination in *Arthropodium cirratum* (Forst. f.) R. Br. are related to seed propagation in nature. A natural population and a cultivated population show identical responses, except that a secondary dormancy can be induced in seed of the natural population after storage for at least 9 months. A period of 3-6 months of after-ripening is required after initiation of seed dispersal to alleviate an innate seed dormancy. This seed dormancy can be attributed to the balance between the 'expansive force' of the embryo and the 'mechanical constraint' of the seed coat. Seed germination occurs over a wide range of environmental conditions. It is more rapid at temperatures of 12-25°C, in darkness or low light intensity, and high water potential. However, many seeds eventually germinate at temperatures from 5-30°C, under high light (295 μmol m^{-2} sec^{-1}) or very low water potential (1.5 mPa). Seed stratification at 2°C for at least 3 weeks induces a secondary dormancy. A novel observation includes the inhibitory effect of diurnal alternating temperatures on germination.

KEYWORDS: *Arthropodium cirratum* - Liliaceae - seed coat dormancy - seed germination - seed ecology.

INTRODUCTION

Arthropodium cirratum (Forst. f.) R. Br. (rengarenga or rock lily), a member of the Liliaceae, is endemic to New Zealand where it naturally inhabits coastal sea cliffs of the North Island and northern Marlborough (Moore & Edgar 1970). It is a perennial species, often forming large colonies, with tufts of semi-drooping evergreen leaves about 50 cm long growing from semi-woody rhizomes. Branching inflorescences up to 1 m tall contain numerous attractive white flowers with yellow anthers. These features make *A. cirratum* a popular species for amenity horticulture, and it is commonly seen throughout New Zealand in areas landscaped with native species (Fisher *et al.* 1970).

In this paper we examine seed dormancy and germination requirements of *A. cirratum*, its response to various environmental parameters and we consider how they may influence seedling establishment of this species in nature.

MATERIALS AND METHODS

SEED COLLECTION

A. cirratum seeds were gathered by placing inflorescences with dehiscing capsules into plastic bags and then shaking them. Single inflorescences were collected from each of 30-40 plants from 2 populations:

1. Oruawairua Island, Marlborough Sounds on 4 February 1980 (from the southern end of Orchard Bay - see Fig. 1 of Conner & Conner 1981). This natural population occupies the typical coastal rocky bluff habitat of *A. cirratum* (Conner *et al.* 1981).

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2. Lincoln College, Canterbury, on 26 April 1980 from a horticultural population of unknown provenance.

SEED STORAGE AND VIABILITY

Seeds were stored at room temperature under dark, dry conditions for up to 7 years. At various times during storage, viability was assessed biochemically using the tetrazolium test (TTC)(Hartmann & Kester 1983), and the standard germination test described below.

GERMINATION TESTS

Seeds were placed on seed germination pads (1 mm thick absorbant cardboard - Lithgow 1959), moistened with distilled water, in 9 cm diameter glass Petri dishes, and incubated in darkness at 20°C. At the initiation of experiments, 0.5 ml of 0.2% (w/v) Orthocide was added to prevent possible fungal contamination. Additional distilled water was added as required to prevent the germination pads from drying out. Germination (radicle emergence by at least 1 mm) was recorded daily, with seeds being removed as they germinated. Unless otherwise stated, all germination tests were performed 6-12 months after seed harvest, with 2 replicates of 50 seeds.

The above protocol was modified as required to examine the influence of the following factors on seed germination in environmentally controlled growth cabinets.

(a) Constant temperatures (0, 5, 10, 12, 15, 20, 25, and 30°C).
(b) Daily alternating temperatures (20/15°C, 25/20°C, 25/15°C with 16 h at the higher and 8 h at the lower temperature) versus constant temperatures (15, 20, 25°C).
(c) Stratification for 3, 6 or 12 weeks at 2°C versus dry storage at room temperature.
(d) Periodic light (16 h at 48 or 295 µmol m^{-2} sec^{-1} followed by 8 h darkness) versus continuous darkness (Petri dishes wrapped in aluminium foil) at 25°C. (This experiment involved 2 replicates of 30 seeds each.)
(e) The presence of gibberellic acid or kinetin at 0, 0.01, 0.1, and 1.0 mM.

GERMINATION IN CONTROLLED WATER POTENTIALS

Seed germination in response to water availability was examined in 2 ways:

(a) Germination (radicle emergence by at least 1 mm) on seed germination pads moistened with a series of mannitol solutions in glass Petri dishes sealed with Parafilm. The mannitol solutions were prepared to correspond to osmotic potentials ranging from 0.0 to -1.5 MPa (Lawlor 1970).

(b) Germination (seedling emergence above soil) in a modified John Innes compost maintained at various water potentials (-0.1, -0.5, -1.0, and -1.5 MPa) by daily watering pots to predetermined weights, based on a water tension versus water content curve (see Conner 1981, Appendix II). Seeds were sown at a depth of 1 cm, and pots were placed in plastic bags to help maintain a constant humidity and prevent excessive evaporation.

SEED SCARIFICATION AND WATER UPTAKE

Seeds were mechanically scarified by cutting through the testa with a sharp scalpel either at the point of radicle emergence, or on the opposite side of the seed. Care was taken to penetrate only the testa, and not to remove any seed fragments when making the incision. Samples of 25 seeds were weighed before and after 24 h imbibition on germination pads, and the percent increase in seed weight calculated.

PRESENTATION AND STATISTICAL ANALYSIS

For convenience the individual experiments were conducted simultaneously on both populations, although in each instance the seed from Oruawairua Island had been in storage 3 months longer than seed from Lincoln College. This was because the time of natural seed dehiscence varied between the populations. Since time in storage had a marked effect on germination (see results), this often meant that germination of Lincoln College seed had virtually finished before germination of Oruawairua Island seed had even started. To simplify the presentation of data, it was necessary to calculate percent germination (% G) after different time periods

for each population. In most instances this was after 10 days for the Lincoln College population and 25 days for the Oruawairua Island population. For these reasons no direct statistical comparison between the populations can be made. Instead analysis of variance was performed separately for each population, with the treatment effects being partitioned into appropriate comparisons (Sokal & Rohlf 1969).

RESULTS

GERMINATION IN RESPONSE TO DRY STORAGE

A. cirratum seeds from both populations were 98-100% viable, as indicated by intense staining in the TTC test, at the time of harvest. However the seed showed very poor germination soon after collection, which greatly improved after 3-6 months dry storage at room temperature (Fig. 1). The Lincoln College population retained rapid germination after 3-15 months storage, whereas germination of the Oruawairua Island population slowed markedly after 6 months storage (Fig. 1). This latter decline in germination resulted from dormancy induced during seed storage rather than a loss of seed viability, since 15 months after harvest over 95% of the seeds intensely stained with tetrazolium and 91% of seeds eventually germinated after extended incubation (100 days).

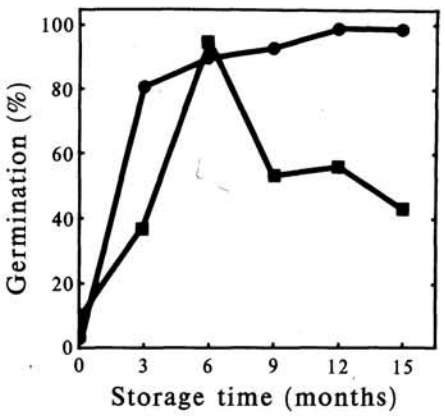

Figure 1. Germination of *A. cirratum* in response to length of dry storage at room temperature after 25 days.
■ Oruawairua Island ● Lincoln College.

Seed viability markedly declined after 5 years dry storage at room temperature. Seeds from the Oruawairua Island population failed to germinate or stain with tetrazolium, whereas less than 15% of those from the Lincoln College population were viable. However the Lincoln College seeds failed to retain any viability after 7 years storage.

GERMINATION IN RESPONSE TO TEMPERATURE

Both populations of *A. cirratum* showed identical germination responses in relation to temperature. Optimum temperature for germination was about 15°C, although rapid germination occurred over the range 12-25°C (Fig. 2). Diurnal fluctuations in temperature markedly inhibited germination compared to each of the constant extremes. This effect was obvious for 5°C alternations, and was even more pronounced at 10°C alternations (Table 1). Stratification of seeds induced a secondary dormancy. This was evident after only 3 weeks moist storage at 2°C, but was considerably more evident after 6 or 12 weeks cold storage (Table 2).

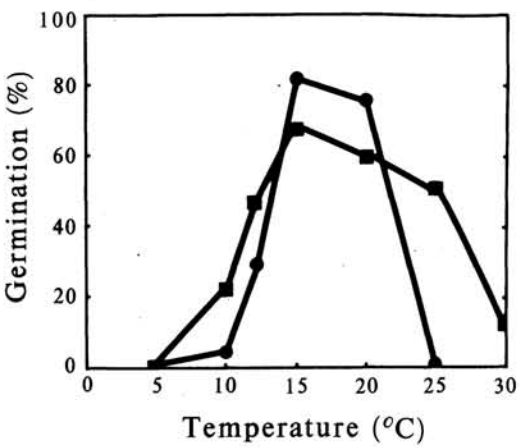

Figure 2. Germination of *A. cirratum* in response to constant temperature.
■ Oruawairua Island (% germination after 25 days);
● Lincoln College (% germination after 10 days).

	Oruawairua Island	Lincoln College
(A) Temperature regime	(% G at day 25)	(% G at day 10)
15°C constant	67	89
20°C constant	60	92
25°C constant	52	37
20/15°C alternating	30	89
25/20°C alternating	25	15
25/15°C alternating	9	5
(B) Analysis off variance[a]		
F_s among constant (2*df*)	5.4^{*}	44.5^{***}
F_s among alternating (2*df*)	11.5^{**}	97.9^{***}
F_s constant vs alternating (1*df*)	209.9^{***}	92.1^{***}
Error mean square (6 *df*)	21	43

[a] *df* - degrees of freedom; ^{ns} - non significance at the 5% probability level; *, **, *** - significance at the 5%, 1% and 0.1% probability level respectively.

Table 1. Germination of *A. cirratum* in response to diurnal alternating temperatures.
(A) Germination under various temperature regimes.
(B) Analysis of variance in which treatment effects have been partitioned into appropriate comparisons.

	Oruawairua Island		Lincoln College	
(A) Stratification time	(% G at day 25)		(% G at day 10)	
	control	stratified	control	stratified
3 weeks	58	22	93	83
6 weeks	56	28	87	2
12 weeks	55	6	91	0
(B) Analysis of variance[a]				
F_s among controls (2*df*)	0.1^{ns}		1.9^{ns}	
F_s among stratified (2*df*)	6.6^{*}		429.3^{***}	
F_s controls vs stratified (1*df*)	109.1^{***}		1205.4^{***}	
Error mean square	39		9.7	

[a] see footnotes of Table 1

Table 2. Germination of *A. cirratum* in response to stratification.
(A) Germination of stratified and non stratified seeds.
(B) Analysis of variance in which treatment effects have been partitioned into appropriate comparisons.

	Oruawairua Island	Lincoln College
(A) Dark/light regime	(% G at day 25)	(% G at day 10)
Continuous dark	58	82
16 h 48 $\mu mol.m^{-2}.sec^{-1}$ 8 h dark	54	89
16 h 295 $\mu mol.m^{-2}.sec^{-1}$ 8 h dark	9	5
(B) Analysis of variance[a]		
F_s treatments (2*df*)	32.3**	99.2**
Error mean square (3*df*)	46.3	45.0

[a] see footnotes of Table 1

Table 3. Germination of *A. cirratum* in response to light.
(A) Germination in various light/dark regimes.
(B) Analysis of variance.

Population and seed treatment	Increase in seed weight upon imbibition(%)[b]	Germination after 1 day (%)[c]	Time between radicle protrusion and first leaf (days)[d]
Oruawairua Island			
untreated control	33.1	0	17.2
testa cut opposite radicle	33.2	0	16.5
testa cut over radicle	32.1	87	17.1
F_s treatments (2*df*)[a]	0.39[ns]	-	0.12[ns]
Error mean square (2*df*)	3.60	-	4.19
Lincoln College			
untreated control	31.1	0	14.9
testa cut opposite radicle	30.9	0	15.8
testa cut over radicle	30.4	92	15.1
F_s treatments (2*df*)[a]	1.18[ns]	-	1.41[ns]
Error mean square (72*df*)	2.58	-	3.91

[a] see footnotes of Table 1
[b] mean ± standard deviation (n = 4 replicates of 25 seeds)
[c] n = 100 seeds
[d] mean ± standard deviation (n = 25 seedlings)

Table 4. Water uptake and germination of *A. cirratum* seeds with and without mechanical scarification via cutting the testa.

GERMINATION IN RESPONSE TO LIGHT

Low light intensity (48 μmol m^{-2} sec^{-1}) had no influence on the germination of *A. cirratum* seeds. However, higher light intensities (295 μmol m^{-2} sec^{-1}) are clearly inhibitory to the germination of seeds from both populations (Table 3), although after extended time (100 days) 32% and 81% of seeds from Oruawairua Island and Lincoln College respectively, germinated under the high light intensity. Seeds left in darkness, without daily examination, showed similar germination after 3 weeks (within 4%) to those repeatedly observed for germination. This establishes that the brief multiple exposures to light throughout the experiments (to record results) did not influence the germination of *A. cirratum*.

GERMINATION IN RESPONSE TO WATER POTENTIAL

Germination of both populations of *A. cirratum* occurred over a wide range of water potentials from very wet (0.0 MPa) to very dry (-1.5 MPa). However radicle emergence in mannitol solutions became progressively slower with decreasing water potential (Fig. 3a). A similar response was observed for seedling appearance above soil of controlled water potentials (Fig. 3b). In this soil approach, the water potential values represent the average effect within pots, with no regard to possible moisture gradients. However, the treatments clearly provided a range of water potentials from very wet to very dry.

After prolonged periods (90 days), greater than 85% and 50% germination was recorded in mannitol solutions and soil respectively for both populations at very low water potentials (-1.5 MPa).

GERMINATION IN RESPONSE TO PLANT GROWTH REGULATORS

Both gibberellic acid and kinetin (0.01-1.0 mM) failed to either promote or inhibit the germination of the two *A. cirratum* populations (data not shown). These growth regulators also failed to overcome the inhibitory effects of high light intensity (295 μmol m^{-2} sec^{-1}), and the dormancy induced by stratification or dry storage

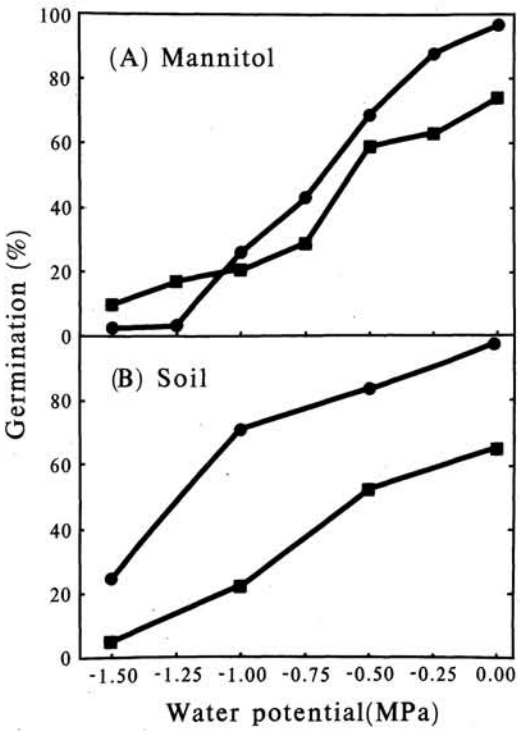

Figure 3. Germination of *A. cirratum* in response to water potential.

A. Radicle emergence in mannitol solutions.
■ Oruawairua Island (% germination after 25 days)
● Lincoln College (% germination after 10 days)

B. Seedling emergence above soil of controlled water potential after 50 days.
■ Oruawairua Island
● Lincoln College

of the Oruawairua Island population at room temperature for 15 months.

GERMINATION IN RESPONSE TO SCARIFICATION

Cutting through the testa of *A. cirratum* seeds at the point from which the radicle emerges, resulted in the immediate germination of most seeds from both populations (Table 4). In contrast, when the testa was cut opposite the point of radicle emergence (or any other position) germination occurred at the same rate as in untreated seeds (seeds started germinating from day 5-11). Both cut and untreated seeds absorb

the same amount of water (Table 4). In both populations, the time between radicle emergence and the appearance of the first leaf was the same in untreated seeds and seeds cut in either position (Table 4).

Cutting the testa over the point of radicle emergence alleviated the dormancy induced by stratification and storing the Oruawairua Island population at room temperature for 15 months. Seeds treated in this manner also germinated immediately when incubated under high light intensity (295 µmol m^{-2} sec^{-1}).

DISCUSSION

Horticultural guidelines for the propagation of New Zealand native plants state that seed of *A. cirratum* readily germinates (Fisher *et al.* 1970). The results of this investigation clearly support these claims. The seeds of both populations of *A. cirratum* germinated over a wide range of temperatures, light and water potentials. Although extreme temperatures (5-10°C and 25-30°C) (Fig. 2), high light intensity (295 µmol m^{-2} sec^{-1}) (Table 3) and drier conditions (Fig. 3) greatly reduced the germination rate, many seeds did germinate after prolonged periods under these conditions. The capacity of *A. cirratum* to eventually germinate in very low water potential (-1.5 MPa) suggests a high level of drought tolerance, since this represents permanent wilting point for most soils (Brady 1984).

Seed dormancy in *A. cirratum* can be clearly attributed to seed coat effects, since cutting the testa over the point of radicle emergence resulted in immediate germination (Table 4). However this seed coat dormancy is not a consequence of an impermeable seed coat. This was demonstrated by cutting the testa in other positions, which had no influence on germination. Also, cut and untreated seeds absorb similar amounts of water (Table 4). Seed coat dormancy in *A. cirratum* is therefore attributed to a balance between the physical force generated by cell expansion during growth of an embryo and the mechanical strength of the testa to resist this pressure. Although this seed dormancy mechanism was once considered to be no more than a rare curiosity (Mayer & Poljakoff-Mayber 1963), it is now well established in a variety of species (Thimann 1977). In *A. cirratum* this dormancy is promoted by high light intensity, seed storage and stratification. After the radicle has emerged from the seed, seedling development continues at the same rate whether or not the testa is cut over the point of radicle emergence (Table 4). This establishes that other forms of dormancy associated with embryo development do not exist in *A. cirratum*.

Both populations of *A. cirratum* showed identical germination response to all except one of the variables examined. In the natural population (Oruawairua Island), secondary dormancy was induced in seed stored for over 6 months under dry conditions at room temperature. This was not apparent in seed from the cultivated population (Lincoln College) (Fig. 1). Such a loss of seed dormancy is typical of plants in cultivation, where a selection pressure is automatically imposed for seeds to germinate immediately after being sown. This results in rapid selection for reduced dormancy (Harlan 1975, Simmonds 1979).

When the environmental constraints on seed germination are considered in conjunction with the dormancy characteristics of *A. cirratum*, a number of conclusions can be made regarding germination strategies that regulate seed propagation in nature. Seed maturation and dispersal occur in late summer-early autumn (February to April). The initial seed dormancy for 0-3 months following seed maturity (Fig. 1) would prevent the majority of seeds germinating prior to winter. Cooler temperatures during winter would not only inhibit germination (Fig. 2), but are also likely to result in the induction of a secondary dormancy period (Table 1). The large majority of seeds would therefore be expected to start germinating with increasing temperatures in spring. This coincides with the *A. cirratum* seeds showing a marked peak in germination potential 6 months after harvest (Fig. 1). Since the release from secondary dormancy in *A. cirratum* occurs only gradually, there is unlikely to be a sudden flush of germination in spring. Instead germination would be expected to occur gradually throughout the growing season of the current, or possibly subsequent years. The ability of seeds to remain dormant and gradually germinate over an extended period is an

extremely important demographic property of seeds (Cook 1980). This decreases the probability of a chance annihilation of a seedling population following simultaneous germination of many seeds (Koller 1964).

When germination does occur, it will be predominantly of seeds under the shelter of existing plants, or of seeds covered in soil or debris, since high light intensities are inhibitory to germination (Table 3). In the exposed coastal environment that *A. cirratum* naturally inhabits, seedling establishment under or near existing plant cover is probably highly desirable for survival and growth.

A novel observation recorded in this study was the inhibitory effect that diurnal fluctuations in temperature had on the germination of *A. cirratum* seeds. Alternating temperatures usually increase the germination potential of seeds (Mayer & Poljakoff-Mayber 1963). Despite an extensive literature search, we have been unable to trace any other example of such a delay in germination in response to alternating temperatures. This response may be of ecological significance to *A. cirratum*, which naturally occupies a narrow habitat range close to the high tide mark on coastal sea cliffs. The 'insulating' effects of the ocean water on temperature extremes would result in minimal diurnal soil temperature fluctuations compared with other sites further from the sea. Furthermore this response to alternating temperatures is also likely to act along with high light intensity in reducing the germination of seed on the surface of exposed sites. Such sites would heat up considerably in direct sunlight and rapidly cool at night compared to more insulated sites under plant cover.

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